

OBSERVATIONS ON THE NESTING HABITS OF COLLETES
STEPHENI TIMBERLAKE

(Hymenoptera:Apoidea)

PAUL D. HURD, JR. AND JERRY A. POWELL

University of California, Berkeley

During the past several spring seasons field parties of the California Insect Survey have made repeated attempts, while collecting on the Colorado Desert of California, to obtain a series of an undescribed bee, the largest *Colletes* known to occur in America north of Mexico. The bee was first recognized from two specimens collected in April, 1952, near Hopkins Well, some 18 miles west of Blythe, Riverside County, California. It was, therefore, one of the goals of a return trip to Hopkins Well this year to secure a series sufficiently large enough to permit characterization of the species. The bee, *Colletes stepheni*, is described in an accompanying paper by P. H. Timberlake (1958), for it was our good fortune not only to collect an adequate series, but also to discover an extensive nesting site.

The nesting area, which was studied April 14 to 17, 1958, is located on the prominent, drifting sand dunes immediately south of U.S. Highway 60-70 just to the east of Hopkins Well, Riverside County, California. The site extended in an arc, some 12 yards in width for approximately 170 yards on the north and west facing slopes of the curving dunes. Within this zone most of the burrows were localized into six principal groups consisting of 39, 28, 22, 22, 15 and 12 burrows. The entire nesting area probably had some 200 burrows active at that time. The drifting sand dunes in the area occupied by the nests are partially held in place by scattered bushes of two predominant perennial plants,¹ Creosote Bush (*Larrea divaricata* Cav.), and a tall dry, clumped grass with the culms 2 to 3 feet in height known as Galleta (*Hilaria rigida* (Thurb.) Benth.). Unusually heavy rains of the preceding winter occasioned a profusion of annual growth consisting primarily of *Oenothera deltoides* Torr. & Frem. and *Psilostrophe cooperi* (Gray) Greene, which also aided in the stabilization of the dune surfaces.

The nests were grouped in unvegetated areas with the range of distance between burrows being about 15 cm. to three meters. The most evident feature of the burrow, which is plugged during

¹ The plant identifications used in this paper were made by Helen K. Sharsmith, University of California Herbarium, Berkeley.

most of the day, is the large and distinctive tumulus that is formed on the downward slope below each nest entrance. As will be noted in the illustration (fig. 1), the fan-shaped mound rather resembles the tailings of a mine shaft.

The nesting area was first discovered late one afternoon when large numbers of the males were seen coursing with an audible hum over the closed burrows. On the subsequent day (April 15) the sequence of this late afternoon flight was observed. The first male was seen at 4:59 p.m. (Pacific Standard Time) and by 5:15 p.m. the main flight had commenced. At this time 20 to 30 males were coursing, some two or three inches above the sand, over one group of nests in an area of approximately 200 square yards. This activity was evident over the entire nesting area. The concentration of individuals continued to increase until by 5:30 p.m. the audible hum was evident. From this time until the sun dropped below the horizon at 5:58 p.m. the flight gradually diminished, continuing to do so through the period of twilight. The last active male was observed at 6:21 p.m., well before dark. At the conclusion of their flight the individuals dispersed to nearby vegetation for the night. Large numbers of them were discovered sleeping on the tall seasoned culms of the Galleta grass where nearly all individuals rested in a head down position clinging with their legs. It is not known whether this was a preferred resting site, but males were not found sleeping elsewhere.

During the main flight occasional small groups (3-6) of males were frequently congregating on the sand, scratching or attempting to dig, tumbling and struggling with one another using their mandibles and legs. Some were seen scratching at the burrow entrance plugs. Often individuals entered depressions in the sand or burrow-like holes and bumped various objects lying about the nesting site, such as small dark plant fragments, an empty wasp cocoon, and frass pellets of the sphinx moth, *Celerio lineata* Linnaeus. One male pounced on a small tenebrionid beetle (*Blapstinus* sp.) as it crawled through the nesting site. Perhaps the most remarkable observation was that involving the males' activity about a dead adult female andrenid bee, *Andrena rozeni* Linsley and MacSwain,² lying on the surface of the sand. The dead *Andrena* was repeatedly tumbled by the *Colletes* males, and several males each in turn attempted to copulate with it by

² Determined by E. G. Linsley and J. W. MacSwain, University of California, Berkeley.

climbing upon its back and actually extruding the genitalia in contact with the tip of the dead female's abdomen.

It is assumed that the purpose of this evening flight is that of seeking out and copulating with the females as they open their burrows. The one copulation that was observed occurred at 6:03 p.m. when several frenzied males were seen at a burrow tumulus where a female was unplugging her burrow. The female was dragged out by two or three struggling males, one of which apparently successfully managed to copulate with her. Almost immediately the other males left, and after several seconds the pair separated, probably due to the intervention of the observer. For some reason, possibly the stage of the nesting activity of the colony, almost no females opened their burrows during the male flight. It would appear likely that females requiring copulation must unplug their burrows while this evening male flight is in progress. However, during the period of observations, nearly all

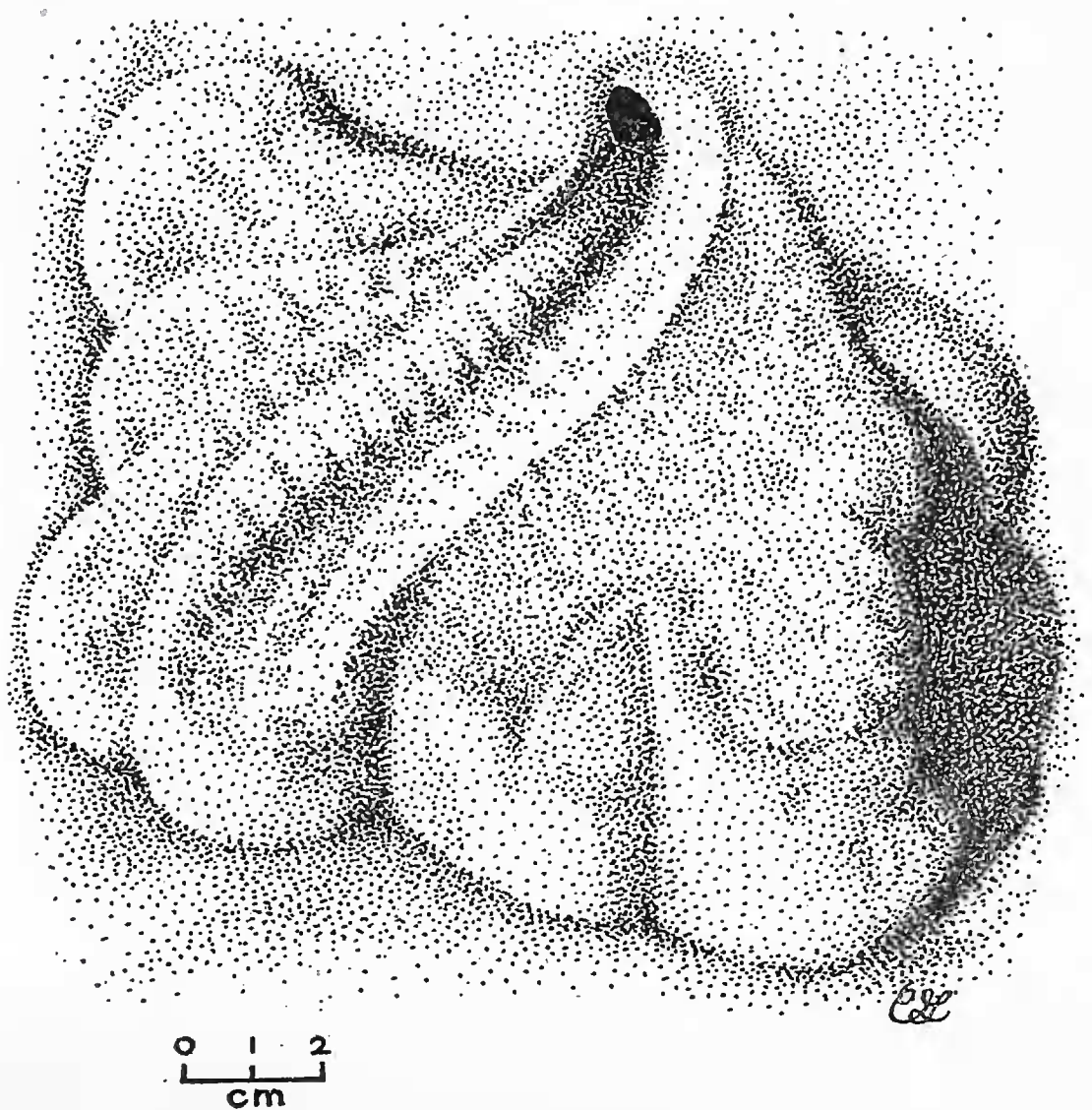


Fig. 1—Burrow tumulus of *Colletes stepheni* Timberlake.

the burrows remained closed for about an hour after the end of the male flight.

Observations revealed that the excavation of the burrows by the females was carried out during the night with the first individual engaged in this activity having been seen at about 7:14 p.m., well after dark. More females continued to open burrows and commence digging as the evening progressed. By 8:00 p.m. 10–20 per cent had begun work, and by 10:30 p.m. the majority of the burrows were unplugged with their occupants active. The digging process was continuous until at least 11:30 p.m., when our investigations were postponed for the night. Observations were suspended between the hours of 11:30 p.m. to 4:30 a.m. and it is not known how long the excavation continued.

On the basis of several bees observed, the digging process seemed to be relatively uniform in pattern. Following the gradual removal of the plug, the female was seen to always back out abdomen first, pushing the excavated sand with her abdomen and hind legs. After three or four trips to the surface, in which small loads of dry sand were deposited near the entrance, successively closer each time, the female backed completely out of the burrow and pushed the accumulation across the surface of the tumulus, forming a depressed trackway (fig. 1). When the pushed sand reached the periphery of the tumulus, it cascaded from the end of the trackway, adding to the steep outer margin of the tailings. This trackway, during the course of an evening's digging, was shifted from side to side across the surface of the tumulus. As the bee backed out, the trackway assumed a characteristic reticulated appearance due to a curious oscillating of the abdomen and legs.

Upon revisiting the nesting site before dawn (4:40 a.m., April 17) the burrows were open. It seems likely that they remained open all night. We assume from females seen by E. G. Linsley, J. W. MacSwain and P. H. Timberlake at the pollen source, Creosote Bush (*Larrea divaricata* Cav.) as early as 4:20 a.m. that the morning's provisioning had already begun. However, judging from activity at the burrows when we arrived and at the height of the provisioning period (5:00 a.m. to 6:30 a.m.) it is presumed that the pollen gathering had begun only shortly before. Since the first pollen-laden females were seen returning at 4:55 a.m. (just at sunup) we know that the first departures had already

occurred. Males were found still sleeping on the culms of *Galleta* while a few other males were flying about the general nesting area.

The time data obtained on the pollen collecting flights are tabulated in Table 1. The flights averaged about 20 minutes and ranged from 12 to 39 minutes. Much of this variation is attributable to differences between individuals, for example female *C* took longer than *A* or *D*. Females when leaving burrows hovered in a small arc a few inches above and downhill from the tumulus before departing. Returning females were seen to either enter without hesitation or to momentarily hover above the entrance before entering the burrow. The plugging was accomplished in stages usually requiring a number of trips to the surface by the female with excavated material. For example, one female which commenced plugging at 6:03 a.m. required seven trips to the surface before the entrance was closed externally at 6:17 a.m.

Table I—Departure (d) and arrival (a) times of pollen trips.
(Pacific Standard Time, A.M.)

observed female	d	a	d	a	d	a	d	a	burrow plugging completed
A.	4:51	5:08	?	5:23	5:26	5:38	?	6:00	7:04
B.	?	5:23	5:25	5:47	5:49	6:13	6:15	6:27	7:12
C.	?	5:15	5:17	5:47	5:49	6:19	6:22	6:47	7:11
D.	?	5:27	?	5:43	5:45	6:00	6:03	6:22	7:04
E.	?	5:31	5:33	6:12	—	—	—	—	6:58
F.	?	5:10	—	—	—	—	—	—	6:17
G.	?	5:29	?	5:46	5:49	6:07	—	—	7:21
H.	?	5:37	?	6:01	6:05	6:36	—	—	7:01

By 7:20 a.m. in one site under study, 21 of the 28 burrows were already plugged. All burrows were closed by 8:00 a.m. Reports from the floral source indicated that the morning activity of the males (nectar) and the females (nectar and pollen) had largely ceased by 6:20 a.m. Apart from the few males seen briefly about the nesting site before sunrise, no male activity comparable to the evening flight took place over the burrows. It is believed that the males spend the day in abandoned burrows or other holes in the dunes. This is suggested in part by their absence on the *Galleta* grass, as well as by numbers of males observed in one instance leaving an abandoned burrow in the evening.

The four burrows excavated for study showed a general similarity in configuration and depth. Individual variation was nonetheless evident in the degree and direction of lateral displace-

ment. The nests were initiated in a substrate consisting of unconsolidated dune sand to a depth of approximately 50 cm. Below this level existed a layer of hard-packed dune sand which when removed remained in consolidated chunks. A moisture layer commenced four or five cm. below the surface and extended about 45 cm., approximately to the upper level of the underlying compacted layer. This situation explains the dry sand being deposited at the surface by the females which were excavating below the moisture level. From the entrance the tunnel, which was about 7 mm. in diameter, progressed inwardly almost horizontal to the surface for about 15 cm. The initial portion of the nesting tube when plugged is filled with sand for about 8–10 cm. from the entrance. Following the horizontal portion the tunnel curved into a nearly vertical drop of 45–50 cm. At about this point the burrow angled away to either the right or left, continuing downward somewhat less steeply to a depth of about 75 cm. from the surface. The final section of the burrow varied considerably between individuals, but in general made a second steep drop before attaining the cell level. The fact that the exposed portion of the tunnel remained intact on the wall of our excavation indicates that the bee may have structurally supported the burrow by some means, but no lining was evident. One burrow successfully excavated was found to be still under construction. The female bee was found at the end of the nesting tube 130 cm. long, some 90 cm. below the surface of the dunes. In another case a single partially provisioned cell was located at the end of the burrow about 98 cm. beneath the dune surface. The apparently unlined cell contained a membranous cellophane-like capsule, provisioned with a viscous liquid mixture of *Larrea* pollen and nectar. No egg was found, however the cell had been partially damaged since the female had been forced backward into it during our digging operation. The tunnel in this instance was estimated to be 140 cm. long and had four angles of 35° to 45° during its course (alternating from sinistral to dextral).

During the course of our study three hymenopterous parasite species were observed in the nesting area. Two of these appeared to have a definite relationship with the bees under study. Nine females of a large undetermined *Sphaerophthalma* [*sensu* Schuster 1958]³ (Mutillidae) were collected crawling on the sand in the

³ Determined by W. E. Ferguson, University of California, Berkeley.

nesting area between 7:20 p.m. and 8:10 p.m., and one of these was taken shortly after it came out of an open *Colletes* burrow. Extensive collecting during several evenings in other areas of the dunes failed to reveal its presence. Another mutillid, *Dasymutilla arenivaga* Mickel, although observed wandering through the nesting site, seems more likely to be associated with bembicine wasps nesting on the dunes. A large ferruginous and undetermined parasitic bee of the genus *Nomada* was seen to enter an open active burrow at 6:55 a.m. and remain within for about 20 seconds. The bee, a female, was collected on its reappearance.

Since *Colletes stephensi* Timberlake is itself so unique and exhibits so unique a nesting behavior, no attempt is made to compare it with any of its congeners. A summary relating to the bionomics of the genus has been provided by Stephen (1954: 155–163). The only North American species of the genus *Colletes* whose nesting habits have been previously reported upon in some detail is the eastern United States *C. inaequalis* Say.

Celeste Green, Scientific Illustrator, University of California, Berkeley, kindly prepared the accompanying figure from photographs taken at the nesting site.

LITERATURE CITED

SCHUSTER, RUDOLPH M.

1958. A revision of the sphaerophthalmine Mutillidae of America north of Mexico. II. Ent. Americana 37:1–130, 7 plates, 3 tables.

STEPHEN, W. P.

1954. A revision of the bee genus *Colletes* in America north of Mexico. (Hymenoptera, Colletidae). Univ. Kansas Sci. Bull., 36:149–527, 87 figs., 8 maps.

TIMBERLAKE, P. H.

1958. A new species of the genus *Colletes* from the Colorado Desert of California (Hymenoptera:Apoidea). Pan-Pacific Ent. 34:143–145.

RECENTLY PUBLISHED

OBSERVATIONS ON THE HABITS OF *STYLOPS PACIFICA* BOHART.

By E. G. Linsley and J. W. MacSwain. University of California Publications in Entomology, Vol. 11, No. 7, pp. 395–430, incl. pls. 51–53, 1 text fig. University of California Press, Berkeley and Los Angeles. April 30, 1957. Price 75 cents.

A fine paper in which some erroneous ideas are corrected and the subject clarified. The illustrations are excellent.